# Niche theory and macropodid nutrition

by J. E. Kinnear and A. R. Main

Department of Fisheries and Wildlife, Wildlife Research Centre, P.O. Box 51, Wanneroo, W.A. 6056
(formerly Zoology Department, University of Western Australia)
Zoology Department, University of Western Australia, Nedlands, W.A. 6009

## Abstract

Arid zones are universally acknowledged to be nutritionally hostile environments; this paper sets out to explain the observed capacities of the "ruminant-like" macropodid marsupials to survive in such environments by relating their nutritional biology to the concept of the niche. New insights are achieved by this approach. The nutritional niche is defined as a subset of the Hutchinson niche space; it is shown that the symbiotic interaction between the pregastric microbes and the host mammal enables the host to occupy an expanded nutritional niche. It is predicted that under specific and well-defined conditions, mammals with pregastric fermentation (PGF—i.e. ruminant and ruminant-like species) are competitively inferior to non-PGF herbivores in a nutritional sense, but they avoid the consequences of this competition by occupying expanded nutritional niches which exclude competitors. This nutritional theme of niche expansion common to all mammals with PGF is shown to be nutritionally flexible allowing specialization in the nutritional niche which is more pronounced than external morphology would indicate.

## Introduction

Humans in arid conditions are impressed by the heat, shortage of water, and absence of shade, and it is natural to believe that arid-zone animals occur where they do because they can handle these stresses. We therefore tend to concentrate our studies on measuring the performance of arid-zone animals under laboratory conditions which are believed to represent in some way field conditions in arid places.

These laboratory studies measure achievement of animals, i.e., what the animal can endure, because when we set up laboratory experiments we take care that the animal cannot behaviourally avoid the conditions we wish to impose on it. The results of these studies are thus measures of survival, but frequently we have no measure of whether the animal experiences such conditions in the field or not.

However, in order to persist, a species must not only endure environmental stresses but also maintain a population, and this is done only when offspring survive and grow to reproductive age. Even this is not sufficient to ensure persistence, because an organism also has to contend with competitors for resources which may be in short supply. Thus three stages are involved: (a) Survival, in which physiological performance may be important but behavioural avoidance may be equally important; (b) Growth, in which nutrition, especially dietary protein, vitamins, essential lipids, minerals and energy, are important; (c) Reproductive success (also dependent on adequate nutrition), which ensures that aging animals are replaced by offspring. These stages are not equally easy to analyse. The first has fewer difficulties and is commonly studied as environmental physiology or ecophysiology. It is generally assumed that the present capacities of animals to maintain life in the face of hot arid conditions represent the culmination of all the selection there has been over the period that has elapsed since the environment became arid.

It is now thought that the onset of aridity occurred much earlier than formerly believed. It appears that a trend towards aridity started in Late Miocene times (Bowler 1976), and was accentuated by climatic oscillations of wet and dry periods in the Quaternary. Associated with these oscillations there is a well-documented extinction of many large marsupials and in those cases where extinction did not occur, selection for smaller-sized species occurred (Bartholomai 1972, 1975; Marshall 1973); but even the smaller forms have continued to disappear as, for example, potoroos were only taken shortly after the settlement of Western Australia and not subsequently. Thus it would appear that although a number of species have become rare or extinct because of European settlement, evidence from fossil and subfossil deposits implies that at the time of the colonisation of Western Australia, the faunal assemblage represented a terminal stage of a long process of extinction and a reduction of faunal diversity which began much earlier.

It is a common observation that when faunal diversity is reduced, the surviving species frequently expand their range or occupy habitats in which they were formerly never found; ecologists describe such situations as competitive release or expansion of the realised niche. For example, the habitat occupied by the quokka *Setonix brachyurus* on Rottnest Island, and the tammar wallaby *Macropus eugenii* on the Abrolhos, is quite unlike the preferred situation on the mainland; both cases seem to indicate habitat expansion made possible in part by the absence of competitors. Another example of ecological release from constraining environmental variables has been observed in the case of kangaroos, as when pastoral water and improved grazing conditions enable kangaroos to increase in numbers (Ealey 1962, 1967; Newsome 1975). But these are exceptions because, in general, there is little evidence to suggest that range expansion has occurred in the case of the surviving fauna, and on this basis we can infer that the present depauperate fauna exists in competitive equilibrium for environmental resources.

We are still left with the question as to why so many species became extinct. And can we, by studying the ability of the faunal elements which survived the extinction, make any statement as to why the current fauna persisted? Was it physiological capacity, reproductive efficiency, nutritional flexibility or behavioural avoidance?

Some of these aspects have been previously dealt with by Main (1968, 1970, 1976, 1978) and Main and Bakker (in press). Here we propose to deal with the physiology of nutrition insofar as this has relevance to the trend to aridity already discussed. We will argue that the dominant herbivorous marsupials—the macropodids, i.e., kangaroos, wallabies, rat kangaroos—have evolved a flexible system of alimentation appropriate to the arid zone which has a recognisable nutritional theme. Moreover, we will attempt to show that this flexible nutritional theme has many variations which have been moulded by competitive interactions as predicted by ecological concepts and the theory of the niche. Finally, we will also attempt to show that the nutritional adaptations displayed by the macropodids have compromised their energetic and reproductive efficiencies.

Accordingly, this paper will not be a literature review of the physiology of desert animals as this subject has been more than adequately covered by recent reviews (Brown 1974, Russell 1974). Instead we propose to introduce a new approach to the nutritional physiology of the macropodid marsupials and then to discuss some of the biological implications of this approach. We will begin our account by introducing some basic concepts of niche theory.

## The niche: an abstractly inhabited hypervolume

Niche is a term that was first used to indicate the role or function of a species in the community. The concept was not well defined, and as a result usage was not precise and the term became almost meaningless. In 1957, the concept of niche acquired elements of mathematical rigour and precision previously unrealised, due to the efforts of G. E. Hutchinson (1957) who conceived of a new way of defining the niche.

In set-theoretic terms, the fundamental niche (N) of a given species is a n-dimensional hypervolume or space. Hutchinson considered all of the environmental and biological factors (not ncessarily independent) that affect the survival of a species, and to every variable or factor he assigned an axis. On each axis he specified arbitrary limits, the limits denoting a region within which a given species can survive and persist.

To illustrate Hutchinson's concept, we will consider two familiar variables that affect the survival of desert herbivores—temperature and available water in plant tissues. A given species will survive and reproduce within a certain range of temperature and water concentration in plant tissues. If these ranges are linearly ordered on a pair of rectangular co-ordinate axes (Fig. 1A), a region (in 2 space) is defined within which the species can persist. In effect we have specified the physiological tolerances of a given species with respect to temperature and available plant water. The concept is generalised by considering all relevant variables, i.e., a third axis would define a volume or 3 space; n-axes would define a hypervolume of n-space and thus a species' *fundamental niche*.

Upon defining the fundamental niche, Hutchinson proceeded to qualify the concept by considering biological interactions (e.g. competition) among organisms. He reasoned that because of biological interactions, a species need not exist within the full extent of its fundamental niche; this contracted niche space, Hutchinson termed the *realised niche*.

An assumption, indeed a biological axiom, states that at equilibrium, no two sympatric species can occupy the same niche space. This assumption is based on the competitive-exclusion principle (see Hardin 1960); we will have occasion to invoke this principle as some important predictions flow from it.

On considering the foregoing, a little reflection reveals that much of the physiological literature represents efforts by physiologists to define a species' fundamental niche. Any studies that characterise a species' tolerance or requirement for an environmental factor can be interpreted as characterising axes or subspaces of a species' fundamental niche. Furthermore, if a physiological adaptation increases the tolerance of an organism to a stressful factor, or lowers the requirement for an environmental variable, then such adaptations may be defined as expanding the fundamental niche. We suggest that this is a useful way of describing the biological significance of physiological adaptations.

The merits of this approach will be particularly apparent when we discuss the biological implications of macropodid nutrition, as some new insights have been gained by applying the above ecological concepts. However, before we do this it will be necessary to describe some background material.

## Early studies on marsupial nutrition

Pioneering studies on macropodid nutrition began when H. Waring approached R. Moir and M. Somers of the Institute of Agriculture about the nutritional significance of the unusually large forestomach of the Rottnest quokka (*Setonix brachyurus*). Their studies revealed that the quokka was "ruminant-like". Bacteria were present in huge numbers in the stomach contents and microbial end-products—volatile fatty acids (VFA)—were found in concentrations comparable to those in domestic ruminants (Moir *et al.* 1956). Subsequent work has amply confirmed their original conclusions, and the ruminant-like physiological convergence has since been extended to other macropodids as well as some eutherians (Moir 1968).

Additional nutritional studies were stimulated by Ealey's (1962, 1967) investigations on the euro or hill kangaroo *(Macropus robustus)* in the Pilbara. This work was initiated in response to the demands of pastoralists to control the euro which was viewed by the industry as a serious economic pest. One of the results of Ealey's research was the finding that pastoral watering points had enabled the euro population to increase. Under natural conditions, the euro population is limited by intraspecific competition for heat refuges in the form of caves in breakaway country—a necessary requirement to maintain water balance. By making free water readily available, the pastoral industry had removed a limiting environmental factor of the niche space of the euro; water balance could be maintained in the absence of heat refuges.

It is significant that the euro population had expanded its realised niche by interacting with a dimension (water) of an agro-ecosystem. Thus the euro is not adapted to the extreme heat as for example are some African gazelles (Taylor 1972) which have expanded their fundamental niches in a physiological way. Survival of the euro under natural conditions is achieved by appropriate behavioural responses in suitable habitats—a tactic which many animals of the arid zone employ.

While there appeared to be no unusual physiological adaptations by the euro to water, studies of their dietary preferences implicated physiology (Storr 1968). Euros were maintaining their numbers on an extremely fibrous low-protein food source (e.g. *Triodia* sp.) which did not support domestic sheep. How the euro population was adapted to such a low-grade nutritional environment remained unknown until G. Brown investigated the problem. His findings were quite remarkable, and his thesis represents a study that was the first of its kind in the sense that no-one had ever determined the nitrogen requirement of a wild species.

The remarkable results obtained from nitrogen-balance trials in the euro revealed the minimum nitrogen requirement of the euro to be 50% lower than that of sheep. The results were fully consistent with the field observations on the diet of the euro, i.e., the euro is physiologically adapted to low protein diets; it has expanded its niche space by having a low requirement for environmental nitrogen (Brown 1964, Brown and Main 1967, Brown 1969).

Perhaps equally as significant was Brown's explanation for the low nitrogen requirement of the euro. He correctly hypothesised that the euro must have a lower standard metabolism, and that the euro recycled urinary nitrogen. Two types of niche expansion are therefore responsible for the lower nitrogen requirement— the first is an expansion of the fundamental niche made possible by a lower rate of metabolism; the second is an interaction of the animal with its stomach micro-organisms, but this represents an expansion of the realised niche. The distinction is a subtle one which has not been recognised, nor have the consequences been appreciated.

## Niche theory and macropodid nutrition

The arid zone is not only noted for its heat and water stresses, but also is characterised by cyclic and unpredictable bursts of primary production followed by long periods of low productivity. During these unproductive periods the standing crop may still be extensive, but the vegetation becomes nutritionally hostile, for one routinely observes in the case of macropods, a loss of body condition (Kinnear and Main 1975) and sometimes heavy mortality in the population (Ealey 1962, Main 1970).

Herbivorous mammals have never directly solved the nutritional challenge of the arid zone. They survive and persist because they have entered into a complex biological association (symbiosis) with microbes. It is significant that they have largely adapted their physiology to maintain the association and to exploit its benefits.

The associations follow two basic patterns: microbes are housed and continuously cultured in two distinct regions of the alimentary tract— either the hindgut (i.e., post-ileo) or both hindgut and foregut. In the latter case, the foregut population is invariably dominant in terms of microbial numbers and gut volume. This design of housing microbial populations in the foregut has been described as pregastric fermentation (PGF) (Moir 1965, 1968), a useful term which rigorously distinguishes PGF mammals from those species that house microbial populations solely in the hindgut (e.g. lagomorphs, perissodactyls).

PGF mammals are represented principally by ruminants and, in the case of marsupials, by the macropodids which are also referred to as being "ruminant-like". Both groups underwent an explosive radiation during middle/late Tertiary times. These evolutionary events, which occurred independently, are correlated with climatic changes that caused seasonal or discontinuous periods in primary production. It is thus a common nutritional solution, and a global phenomenon, with many variations on a theme.

The biology of this nutritional theme of housing a microbial fermentation system in the foregut has in our view never been adequately

explained nor the purpose understood. This is so despite intensive research by nutritional physiologists and animal scientists; it is generally believed that PGF is primarily an adaptation which enables the host animal to exploit fibrous (cellulosic) plant structures as a source of energy.

The rumen and its microbes are also acknowledged to have the properties of an ecosystem. Some attempts have been made to analyse the system as such, but these attempts have not yielded any fresh insights. However, new insights and properties emerge when this biological association is interpreted in terms of niche theory.

### The nutritional niche

The generality of Hutchinson's fundamental niche concept allows one to partition the fundamental niche into subsets of axes. We define the *fundamental nutritional niche* as a subset of axes restricted to those axes representing nutrient variables (e.g., essential amino acids, carbon, phosphorus, essential lipids, vitamins, $H_2O$, etc.) essential to the persistence of a species.

It follows from the above that, if a species is to occupy a niche, there has to be a correspondence between a species' nutrient requirement (NR) and its nutritional niche space (NNS). In abstract terms this means a species must be able to map its NR set into an NNS set. If a species cannot perform this mapping then in concrete terms its nutrient source is lacking in nutrition in one or more ways; persistence is therefore not possible.

### Competition, niche and PGF

A species may be capable of mapping its nutritional requirements into a nutritional niche space, but it can be prevented from occupying a niche space by more efficient competitors. This leads us to examine the competitive abilities of mammals with PGF; we will first consider the theoretical aspects and then we will review the available evidence.

The events that occur in the pregastric diverticulae are usually referred to as "digestion", but this is clearly an inappropriate word; a more accurate description of the processes that occur is *decomposition*. Food of PGF mammals is not initially digested, but is partially decomposed (to varying degrees) by microbes; associated with these events are the growth and maintenance of a microbial population—the pregastric culture.

One of the consequences of microbial decomposition is that some of the dietary components are rendered digestible (e.g. fibre) while other components can be improved in nutritive value (e.g. the essential amino-N and vitamin content); on the debit side, decomposition, as the term implies, leads to energy losses and mineralisation of the host's food. It is for these reasons that we observe the presence of the decomposition products—$NH_4$, $H_2S$, $CH_4$ and $CO_2$ —in the stomach diverticulae.

To emphasise the above, we can say that ruminants and their analogues do not initially digest their food—they rot it, or at least a major part of it. In order to achieve this, these mammals have domesticated microbes and as a consequence they have acquired a unique trophic level (Kinnear and Main 1975).

In acquiring a microbial trophic level PGF mammals have increased the links in their food chain. We recognise: plants → bacteria → protozoa (if present) → mammal. If this were all we knew about these animals, we could still confidently predict on the basis of trophic energetics (and thermodynamics) that macropodids, ruminants, etc., could not possibly be as productive as non-ruminant animals. This is to be expected because productivity calculations must reckon with an additional trophic level, and the inevitable losses associated with the energy and material transfer between trophic levels. The losses are not as great as that observed in more conventional food chains because of the anaerobic (fermentative) properties of the microbial trophic level; nonetheless, as we will show, the losses are still appreciable.

Our trophic analysis has led us to predict that ruminants and their analogues are comparatively inefficient at transforming food into animal biomass. This conclusion is consistent with the experimental evidence—indeed it is an acknowledged fact in the field of animal production (Reid 1970). For example, Armstrong and Blaxter (1961) demonstrated that carbohydrate yields 11 to 30% more energy for production when digested post-ruminally than when decomposed in the rumen. Similar results occur with regard to protein utilization by ruminants. In reviewing this aspect, Smith (1975) concludes: "It seems that the degradation of food protein in the rumen and the use of the products for the synthesis of microbial protein (even though this may be of high biological value) is a very inefficient and wasteful means of using protein resources." In recognition of these inefficiencies it is not surprising therefore to note that animal scientists are endeavouring to develop feeding regimens which enable the rumen microbes to be bypassed (Owens and Isaacson 1977).

To summarise our discussion to this point, we have shown that PGF mammals are relatively inefficient in converting food resources into animal biomass. But this conclusion makes one uneasy for it seems to create a paradox. Given that PGF mammals suffer from measurable inefficiencies, how can we explain the success of the group? What has happened must be this: these animals have made energetic and nutritional compromises in exchange for the ability to exploit and colonise niches that nutritionally exclude most other mammals with different alimentary systems; in other words, they do not compete with non-PGF herbivores for the same sort of food.

## The nutritional niche space of mammals with PGF

Since we have reached the conclusion that PGF mammals cannot compete with non-PGF herbivores, we have raised the question—What is their nutritional niche?

Now the symbiosis between the microbial trophic level and the host animal is a biological interaction, and according to Hutchinson (1957) biological interactions affect the dimensions of the niche hypervolume. Competition is known to contract the niche hypervolume while the converse—symbiosis, which is really negative competition—should therefore expand the niche space. Thus mammals with PGF should be capable of occupying expanded niches. Again the literature supports our predictions—consider the following evidence.

Nutritional niche expansion means that an organism can lower its requirement for a nutrient or increase its tolerance to excess of a nutrient or both. There are many examples of this in the ruminant literature, and perhaps the most impressive examples are the demonstrations which show that domestic ruminants can be maintained in a healthy and productive state when fed diets containing non-protein nitrogen (NPN) as a sole replacement for protein N. Virtanen's (1967) long-term feeding trials with high-yielding milk cows are outstanding examples of a ruminant's ability to eat foods deficient in essential nutrients, i.e. essential amino acids, water-soluble vitamins and essential lipids. With regard to other ruminant-like mammals little work has been done, but Brown (1964, 1969) replaced part of the protein N with urea N (30% of N intake) and kangaroos maintained N-balance. The evidence for the recycling of N by camels (Schmidt-Nielsen et al. 1957) and by wallabies (Kinnear and Main 1975) is indicative of NPN utilisation. Recycling of N, of course, is another example of niche expansion —it lowers the environmental nitrogen requirements of an animal.

We have so far focused our discussion on essential nutrients, pointing out that the pregastric microbial/mammal symbiosis has resulted in niche expansion by eliminating the need for an array of essential nutrients. But mammals with PGF can also use microbes to detoxify plant poisons (e.g. oxalates, alkaloids; Freeland and Janzen 1974), which also results in niche expansion because the microbes have extended the host's tolerances to toxic substances in the food.

It should be stressed that the foregut symbiosis has expanded the realised nutritional niche, and has not affected the host's fundamental nutritional niche. Ruminants still require a full array of preformed essential nutrients; without their pregastric microbes they would require a balanced diet complete in all respects.

### Evidence for nutritional niche expansion

Nutritional niche expansion means that under natural conditions, PGF mammals should be eating foods that are unnutritious in one or more ways. The evidence supporting this prediction is sparse for the simple reason that dietary studies on wild herbivores have been limited to what an animal eats, and occasionally to the gross chemical composition of the diet, e.g. nitrogen, lipids, fibre, minerals, etc. What is necessary to prove our predictions are dietary analyses which measure the essential amino acids, vitamins, essential lipids and toxic substances in an animal's natural diet.

Unfortunately, these analyses are difficult to perform, for they require sophisticated equipment and technical expertise; furthermore, there are also technical difficulties in the field because it is difficult in most instances to define what plants a herbivore is eating, the amounts consumed, as well as the digestibility. In view of this situation, what seemed obviously necessary to us was to find a ruminant-like animal with simple well-defined dietary habits. We were fortunate in finding such an animal in the woylie or brush-tailed rat kangaroo (Bettongia penicillata).

In a study of the ecology of woylies near Manjimup, Western Australia, P. Christensen (1977) discovered that woylies dig up and eat small pebble-sized fungi. We also discovered from stomach content analyses that woylies were eating a gum exudate from the trunk of Hakea sp. There was no evidence that woylies were eating green plants or fibrous materials of any kind (Kinnear et al. in prep.). Analysis of these dietary items revealed that the gum contained no detectable nitrogen and that the fungi were deficient in the essential amino acid (EAA) lysine, but in addition, the EAA methionine was in excess. Hence, not only do we find that woylies are eating a lysine-deficient protein source, but also we find that the protein source has an amino acid imbalance. By known standards of mammalian nutrition woylies, as predicted, are eating unnutritious foods but are meeting their nutritional requirements as the result of microbial synthesis.

### Competitive inadequacies of PGF mammals

In nature, niche theory predicts that we should observe mammals with PGF occupying niches that exclude other herbivorous mammals with different alimentary systems. But they also will be excluded from nutritional niches—in particular, those niches which provide nutritionally balanced foods. This does not mean that mammals with PGF will not thrive on nutritious diets for they will, but because of their trophic status, it means they will utilise such foods inefficiently relative to non-PGF competitors and thus they will be excluded from such niches.

There are, however, conceivable circumstances where dietary analyses may reveal that the foods eaten by some PGF mammals are balanced and nutritious. We have so far conceived of four situations:

(1) The food may be nutritionally complete, but contains toxic substances that are subject to microbial degradation.

(2) Nutritious foods are not limiting, i.e. a surplus exists.

(3) PGF mammals may occupy nutritionally complete niches during seasonal periods, i.e. the growing season.

(4) Competitors may be absent.

To illustrate the niche space of PGF mammals, both in the absence and presence of competitors, we have presented a series of figures representing the nutritional niche space for two dimensions only. In the absence of competition we observe simple niche expansion; in the presence of competitors, PGF animals are excluded from an area of the two-dimensional niche space (Fig. 1).
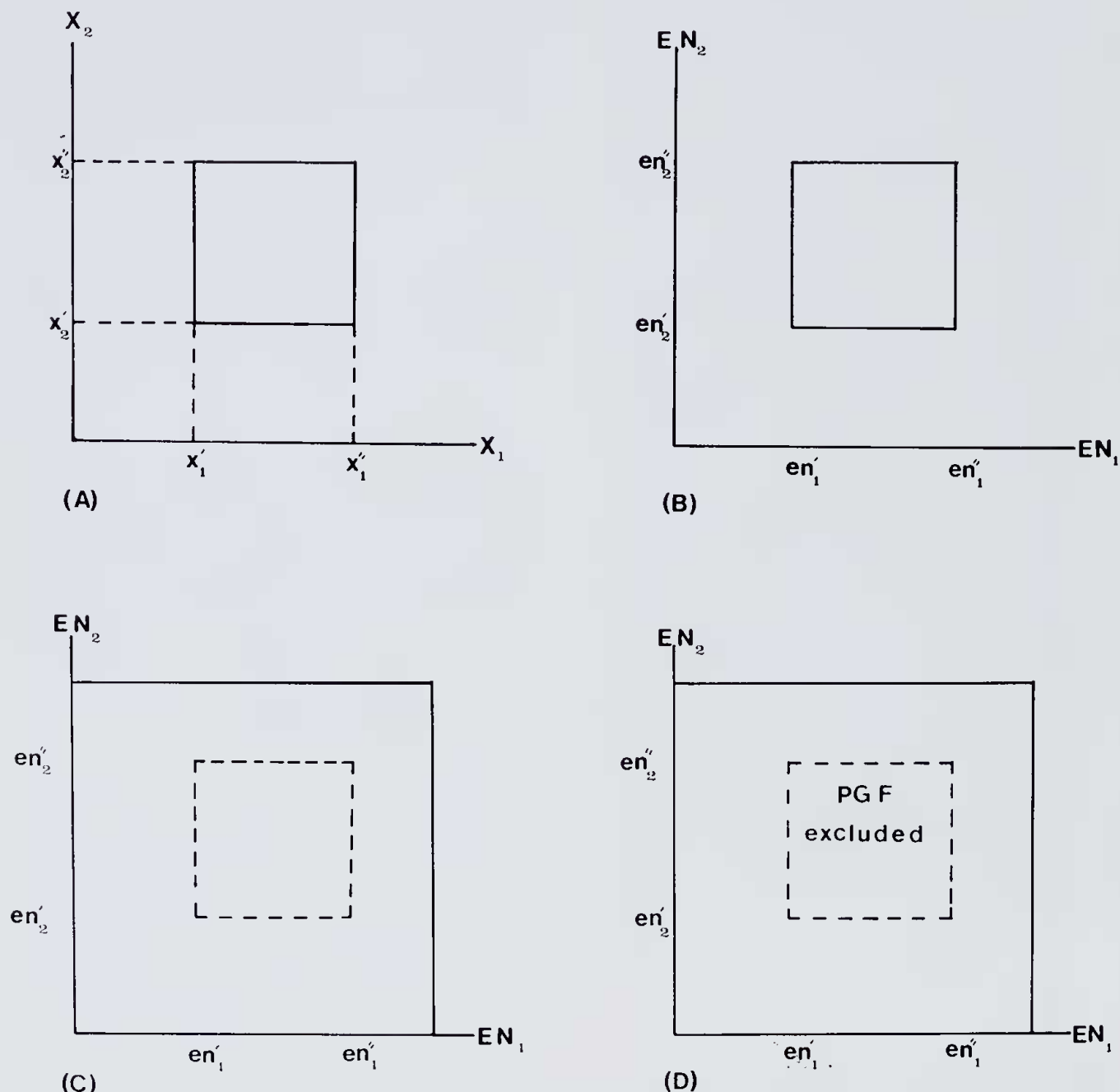


Figure 1.—The niche space restricted to two dimensions for the purpose of illustration (the concept is generalised to n-dimensions). A.—Hutchinson's fundamental niche: factors or variables affecting a given species are linearly ordered on a pair of rectangular axes and the limits $X''_1 - X'_1$ and $X''_2 - X'_2$ define an area (a 2-space) within which a species can survive and persist. B.—The fundamental nutritional niche: two essential nutrients are linearly ordered and the limits ($en''_1$, $en'_1$ etc.) denote an area within which a species survives and persists. C.—The nutritional niche space of a PGF species; the symbiotic interaction results in simple niche expansion in the absence of non-PGF competitors. The inner area represents the fundamental nutritional niche. D.—The nutritional niche space of PGF species under competition with non-PGF species. PGF species are excluded from regions of their fundamental niche space because they are competitively inferior.

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## Competitive interactions between PGF mammals

An immense number of feeding trials involving domestic ruminants has revealed that these animals possess an extremely versatile and adaptable alimentary system, for they have been fed an incredible array of foodstuffs—from newsprint to anchovies. These animals seem capable of eating almost anything, anywhere; their system of alimentation would seem to be the ultimate nutritional solution.

But such impressions are tempered when viewed from an ecological perspective, for ecological theory demands that co-existing species must avoid excessive niche overlap. We should therefore expect and observe niche partitioning of food resources by sympatric species of mammals with PGF. Furthermore, as a corollary, we should expect to observe specialisations in physiology and morphology.

Recent studies have borne out these ecological predictions. Hofmann (1973) has produced an impressive monograph on the African ruminants which describes, in great detail, the different morphological adaptations of the rumen which are correlated with dietary preferences. Hofmann has related stomach structure to the type of food eaten, and he has arranged a large number of African species into three major groups; (a) concentrate feeders—low fibre/succulent diets; (b) roughage feeders—fibrous diets; and (c) concentrate/roughage feeders—i.e. species that eat either foods depending on whatever is seasonally available.

Less information on nutritional-niche partitioning exists for the ruminant-like macropodids but from the available information a similar pattern is emerging. For example, the woylie rat-kangaroo stomach differs substantially from that of wallabies and kangaroos; moreover it is a concentrate feeder (as is the Tasmanian potoroo—Guiler 1971) which ensures that it does not overlap or compete with the three species of macropods using the same habitat (Kinnear *et al.* in prep.).
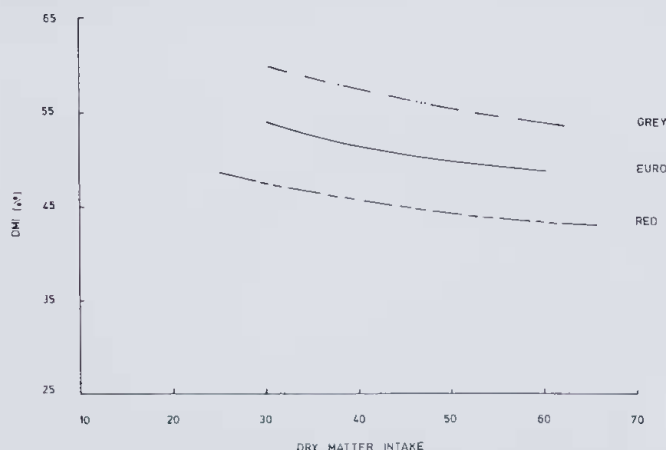
With respect to physiological adaptation and specialisation, differences between the three common species of kangaroos have been documented by Prince (1976). In comparative feeding trials, a standard diet containing fibre was fed to western grey kangaroos *(Macropus fuliginosus)*, red kangaroos *(Megaleia rufa)* and euros; appreciable differences in digestive efficiencies were noted.

The differences are illustrated in Figure 2 where it is evident that the three species differ significantly in their abilities to extract digestible energy from fibrous diets. The red kangaroo is least efficient in obtaining energy from fibre, which means that it must seek out nutritional niches that provide low-fibre foods; in the wild, they are known to do this (Newsome 1975). The opposite extreme is the grey kangaroo which is the most efficient, and Prince points out that the grey, which has a southern distribution, is more subject to cold stress (due to low temperatures and winter rains), and hence the ability to obtain more energy from fibre is an adaptive specialisation to the environment and probably necessary to assure reproductive success. Finally, the euro which is predominantly northern in its distribution (summer rainfall) must also contend with fibre but it can afford to be less efficient.

The prevailing view held by most animal scientists is that the rumen has evolved to cope with fibrous foods. But it is now clear that this view is untenable because PGF mammals eat a wide array of plant materials, many of which are low in fibre. Hofmann's study shows that the fibre-consuming ruminants are merely specialists and we also observe the same sort of specialisation in the case of macropods, i.e. the grey kangaroo and the euro.

Niche theory provides a more general explanation: the function and purpose of PGF is to allow these animals to occupy expanded nutritional niches. At this stage (apart from our woylie study) we cannot support this explanation by factual data because the need for such data has not been recognised, and hence it has not been systematically collected. We hope that this challenge will be taken up.

## Discussion

There seems to be little reason to doubt that pregastric fermentation is indeed a flexible system of alimentation that has been moulded by the pressures of natural selection and competition. We observe a plethora of species (ca. 50 species of marsupials and > 200 eutherian) frequently existing sympatrically in closely-knit associations that seem to defy the competitive exclusion principle. Mammals with PGF are the dominant vertebrate grazer/browsers throughout the world in contrast to the hindgut-fermenting mammals which are relict survivors of a previously dominant group (Moir 1965).

The climatic factors associated with the rise of PGF mammals are cold temperatures and aridity which do not favour continuous plant growth. This forced mammals to satisfy their complex nutritional requirements from vegeta-



Figure 2.—The performance of 3 species of kangaroo in digesting fibrous diets. As dry matter intakes (dry matter wt. $kg^{0.75}$) increase, the percentage of dry matter digested (DMI (%)) tends to decline slightly for all species, but the significant points are the differences between the 3 species in extracting digestible energy from fibrous diets (after Prince 1976—with permission).

tion that was either in a state of dormancy, senescent, or dead. The PGF mammals solved this nutritional challenge in a peculiar way— they largely abandoned herbivory by acquiring a decomposer trophic level which they housed in their forestomachs.

It is this microbial trophic level which imparts nutritional flexibility and which also enables nutritional specialisation. The key to the success of PGF mammals has been the near abandonment of herbivory in favour of linking their food chain to a captive-decomposer trophic level. A significant feature of this trophic level is its affinities with the soil-decomposer ecosystem (Hungate 1960), for such comparisons indicate that PGF mammals have domesticated anaerobic soil micro-organisms which have retained their ecological function—that of decomposing organic matter. When these relationships are recognised and appreciated, it is easy to understand why macropods of the arid zone can survive for extended periods while consuming drought-affected vegetation that is nutritionally equivalent to plant litter.

However, this nutritional theme of housing a microbial trophic level in the foregut is not without its shortcomings for there are competitive and energetic disadvantages. PGF mammals are inherently less efficient in converting and transforming food into animal biomass and, moreover, this inefficiency would seem to have reproductive consequences.

If one surveys the mammalian literature (e.g. Walker 1975) for data on fecundity, a pattern emerges: eutherian mammals with PGF usually bear 1-2 young and this is so regardless of size; macropodid marsupials are uniformly consistent in that they give birth to only one young at a time. Thus it would appear that mammals with PGF have difficulty in allocating their food resources to the production of young; this characteristic is in sharp contrast to the reproductive performance of some non-PGF herbivores, e.g. the rabbit and many rodents.

The macropodid marsupials are further handicapped energetically for reasons that they have a lower metabolic rate (MR) relative to most eutherians (Dawson and Hulbert 1969, Kinnear and Shield 1975). Dawson (1973) has advanced the view that marsupials are energetically primitive, but such views do not help to explain why so many eutherians find it advantageous to generate metabolic power and heat in excess of their homeothermic requirements.

Kinnear and Shield (1975) suggest some advantages: "A high metabolic rate enables rapid synthesis and storage of energy as well as accelerated neonatal development and growth during favourable periods. All of these would be advantages to an animal facing future energy stress." The authors cite as an example the MR of the white-tailed deer (Odocoileus virginianus) which is up to twice as high in summer than winter. This reduction in MR allows for a slower rate of utilisation of stored energy reserves which are rapidly accumulated during peaks of primary production during summer.

Metabolism is an adaptive physiological parameter which not only provides heat to maintain a mammal's body temperature but also determines an animal's biosynthetic potential, i.e. the rate at which it can create biomass. With this point in mind we can appreciate the shortcomings in combining the energetic inefficiencies associated with PGF with a marsupial rate of metabolism, and this would seem to have some relevance to the extinction of the giant macropodids. These species did not survive the climatic oscillations of wet and dry periods in the Quaternary which were superimposed on an overall trend of increasing aridity. The periods of primary production favouring reproduction and growth would have been too short for recruitment because these giant and metabolically sluggish marsupials would have lacked sufficient biosynthetic power to maintain a population. It is significant that the surviving macropodid descendants are smaller-sized species and, moreover, they are sexually dimorphic with the female being smaller and becoming sexually mature at an earlier age than the male.

Thus, in the case of extant kangaroos, each species has adults of two sizes, and when several species occur together as in the Goldfields region of Western Australia where the red, euro and grey are found, there are effectively adults of six size classes. The reason for the containment of these species within their ranges and realised niches requires further study, as Main (1978) has suggested for the western and eastern grey Kangaroos in south-eastern Australia. Should such studies reveal, as seems likely, that habitat specialisation and not inter-species competition is the regulating factor, then habitat specialisation and the nutritional niche of each species are much more highly developed than external morphology would suggest.

From the above reasoning on habitat and niche specialisation, it would seem to follow that habitat alteration and not competition caused past extinctions, and conversely the extant or successful species persisted because they can match their needs even when dietary resources are of poor quality, and so survive to reproduce.

We conclude our account on the following points: within the aerobic zones of the biosphere there are no empty nutritional niches, for all primary production on balance is utilised by consumers or decomposers. Extinction of faunas therefore does not necessarily create or open up nutritional niches, for such niches can be partitioned in a different manner until a new equilibrium is reached between consumers and decomposers. Nutritional niches disappear with the extinction of plant species and communities and, conversely, new niches arise when new plant communities evolve.

It is noteworthy that in arid and semi-arid Australia the one ungrazed habitat is acacia scrub extending from a sandy coastal situation inland to the mulga scrub. No marsupial survived to exploit this nutritional niche yet, this habitat with its tall acacia should have been within the range of the giant marsupials, many

of which are believed to have been browsers. Thus while the Australian fauna has many parallels with its eutherian counterparts, it is significant that the present fauna has no equivalents to the large African browsers, e.g. the Giraffidae. Apparently, the large macropod browsers were incapable of adapting to aridity by dwarfing as in other macropods (Main 1978), because smaller animals are undoubtedly denied the browse on trees and shrubs.

Elsewhere the eutherian browsers persisted in the face of increasing aridity, often by using water holes (Leuthold 1977), and it is significant that when such large species were released in Australia, e.g. the feral ungulates such as the camel, they have successfully colonised the acacia habitat.

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